POLLINATION NETWORKS OF THE HIGH ARCTIC

– ADDING A FUNCTIONAL PERSPECTIVE

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ACADEMIC DISSERTATION

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CONTENTS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I Mikko Tiusanen, Paul D. N. Hebert, Niels Martin Schmidt & Tomas Roslin (2016) **One fly to rule them all – Muscid flies are the key pollinators in the Arctic.** Proceeding of the Royal Society B, 283, 20161271.

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CONTRIBUTIONS

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Original idea	MT, TR	MT, TR	MT, TR
Design	MT, TR	MT, BH, TR	MT, TR
Data Collection	MT, TR	MT, I	MT
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ABSTRACT

Global environmental changes, e.g. fragmentation of habitats and climate warming, are disrupting ecosystems worldwide. These man-induced environmental changes have caused a strong decline in biodiversity, which is hampering the provisioning of ecosystem services. For instance, flying insects and pollinators have declined, especially in industrialized countries, with potentially devastating consequences. However, the impacts of these changes are not easy to predict, since we are missing essential information on how the structure of plant-pollinator networks is actually related to their functioning. In this thesis, I examine such relations in the context of pollination services in the Arctic.

Arctic pollination networks are less diverse than the ones of lower latitudes and, thus, they provide a good opportunity to reveal the basics of the structure and functioning of plant–pollinator interactions. To dissect Arctic pollination networks, I was interested in which plants and pollinators are the most abundant and which are most important in contributing to the functioning of the network. Furthermore, I examined how the species composition of the pollination networks relate to their functioning. In order to achieve a broader perspective, I studied pan-Arctic variation in the pollination networks and their functioning. To further account for the warming climate and its effects on species phenology, I also monitored seasonal patterns in the pollination networks and in their functioning. The resultant thesis work consists of three independent chapters on arctic pollination networks and their functioning.

In Chapter **I**, I found the muscid flies to be key contributors to arctic pollination. At the species level, a single muscid fly species, *Spilogona sanctipauli*, proved to increase the seed set of *Dryas*. Meanwhile, *Dryas* itself emerged as a key species in the high arctic flower visiting network, with two thirds (185 species) of all the local insect fauna visiting its flowers. A single plant species is thus tying together the whole ecosystem.

In Chapter **II**, I discovered remarkable species diversity and spatial species turnover (β-diversity) among arctic pollinator communities. Across 15 locations sampled, I found a total of 1,360 flower-visiting species. Despite relatively high species richness of local communities, each community was dominated by only a few species, the identity of which differed among sites. In general, local species richness increased with increasing annual temperature and precipitation of the site. In addition, community structure wore signs of being shaped by post glacial dispersion patterns, where Eurasian and Alaskan communities were isolated from northeast American communities. Phylogenetic diversity was also highest close to known glacial refugia. Thus overall, this chapter showed the remaining legacy of large-scale historical and climatic factors in current community structure.

In Chapter **III**, I found evidence of the effects of a short pulse of flowering on competition within pollination networks. During the flowering peak of *Dryas*, other flowering species received hardly any visits, achieved only reduced seed set and gained less access to pollen transport by pollinators. The latter pattern, as detected in pollinator pollen loads, suggests that the species-specific amount of pollen transported by flower-visitors is actually controlled by the flowering of the dominant plant species rather than by the abundance of other plant species themselves.

Overall, my thesis reveals that the relatively diverse arctic pollination networks are highly dominated by a few species only, and that this pattern applies to both plants and insects. Given the strong effects of this dominance on both ecosystem functioning and competition for pollination, recently-observed declines in the abundance of key pollinators and an increasing mismatch between plants and pollinators at Zackenberg may further accentuate current patterns of competition. Notably, similar patterns are likely found in other systems also dominated by few species only, e.g. in agricultural landscapes as dominated by monocultures of crop plants and honey bees. As climate warming continues, along with other environmental changes and a decline of pollinators, insect-pollinated plant species may be facing severe challenges both in the Arctic and at lower latitudes.

1. INTRODUCTION

1.1. Pollination is a key process

Pollination is an essential part of the ecosystems of Earth. Most terrestrial biodiversity is directly or indirectly tied to pollination networks, where insects interact with flowering plants. It has been estimated that 87% of all the plants (even up to 99% in tropics) are insect pollinated, and that most of all insects are visiting flowers and could be considered potential pollinators (Olesen and Jordano, 2002; Ollerton, Winfree and Tarrant, 2011). In addition, pollinators have a crucial role in crop production worldwide: 80% of crop plant species and 35% of total crop production are pollinator-dependent (Klein *et al.*, 2007). Furthermore, the essential role of pollinators on crop yield cannot be compensated by other means, such as fertilization or augmented pest control (Motzke *et al.*, 2015).

Given the global importance of pollinators and the recent declines observed in flying insects in general (Biesmeijer *et al.*, 2006; Hallmann *et al.*, 2017; Loboda *et al.*, 2017) and in economically important pollinators in particular (Potts, Roberts, *et al.*, 2010), understanding pollination networks and their functioning becomes an urgent challenge. As man-induced environmental changes remain the main causes for the biodiversity decline, understanding the effects of environmental change on the network is essential (Heywood, 1992; Bartomeus *et al.*, 2018). In the Arctic, the globally most ubiquitous threat, climate warming, is progressing faster than at lower latitudes. Thus, studies of Arctic pollination under climate change provide opportunities for general insights into phenomena related to pollination and ecosystem functioning under massive environmental change.

1.2. Pollination networks and their functioning

During the last few decades, our understanding of ecosystems has expanded at an increasing pace. Advances in computer sciences and in molecular methods have provided us with a completely new tool box for monitoring and understanding fundamental processes in nature. In general, higher biodiversity, i.e. more species, are associated with increased ecosystem functioning and provisioning of ecosystem services (e.g. Hooper, Chapin and Ewel, 2005; Isbell *et al.*, 2011; Wang and Brose, 2018). The mechanisms, however, partly remain to be established. Under natural conditions, most networks of interactions are simply too diverse to allow the dissection of contributions from individual nodes and links within the networks. Thus, current descriptions of biodiversity versus ecosystem functioning are mainly focused on descriptions of overall community or network structures – with little scope for functional interpretation of individual links. This lack of knowledge offers a major hurdle for understanding ecosystem-level consequences of global change (Cardinale *et al.*, 2012).

Biodiversity is thought to improve ecosystem functioning by effects related to either complementarity or sampling (Tilman *et al.*, 1997, 2001; Loreau *et al.*, 2001; Hooper, Chapin and Ewel, 2005; Cardinale *et al.*, 2012). According to the complementary hypothesis, an increasing number of species will generate facilitation, allowing the component species to use up the local resources more completely (e.g. Tilman *et al.*, 1997, 2001; Hooper, Chapin and Ewel, 2005). According to the sampling hypothesis, picking a high number of species will increase the probability of including particularly efficient species in the community (even in the absence of any facilitation effects; Tilman *et al.*, 1997, 2001; Slade *et al.*, 2007). The main difference between these two hypotheses thus relates to the relative role of individual species. While the complementary hypothesis emphasizes the number of species in itself, the sampling hypothesis stresses the presence of certain, particularly efficient species or functional groups as the main driving force behind ecosystem functioning.

In terms of pollination, biodiversity as such may not be particularly important for ecosystem functioning or pollination services (Kleijn *et al.*, 2015). Even in diverse plant-pollinator networks, the main part of pollination is often carried out by the few most common species. The most important species is sometimes as much as 16 times more efficient than the average species (Kleijn *et al.*, 2015). The abundance and functional traits of species define their importance in the pollination networks (Coux *et al.*, 2016), and in terms of crop yield, the functional traits of pollinators and the diversity of such traits is more important than the number of pollinator species (Fontaine *et al.*, 2005; Hoehn *et al.*, 2008; Blüthgen and Klein, 2011; Blitzer *et al.*, 2016; Rader *et al.*, 2016). On the other hand, even a large number of domesticated honey bees is not enough, but other pollinators are also required for optimal seed set (Garibaldi *et al.*, 2013; Blitzer *et al.*, 2016; Rader *et al.*, 2016). On top of all the biotic features (pollination), abiotic features (e.g. water and nutrients) as well as interactions between biotic and abiotic features are also important in determining the productivity of plants (Klein *et al.*, 2015). Thus, the functional role of a

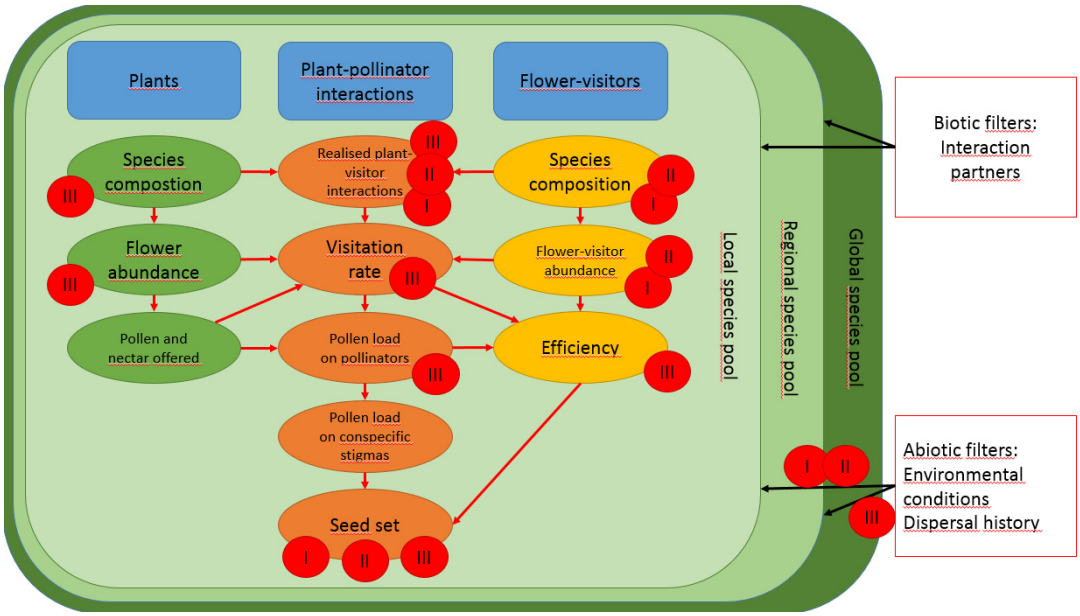

Figure 1. A general framework for the assembly of pollination networks, and links between resultant structure and functioning. The large green boxes represent the global, regional and local species pools, respectively, and the black arrows the biotic and abiotic filters restricting the number of species at each of these levels. The ovals within the local species pool identifies different factors affecting the structure of pollination networks and their functioning. Green, yellow and orange ovals represent the important factors related to plants, flower-visitors and the interactions between these two, respectively. Red arrows represent causalities between the factors. The labels on the red circles indicate the chapters of this thesis which address the factor next to the circles.

single pollinator could vary under different biotic and environmental conditions (e.g. Brittain, Kremen and Klein, 2013).

While the main part of the pollination function may rely on the few most common species (see above), added diversity of functional groups may potentially buffer pollination under changing environmental conditions (Brittain, Kremen and Klein, 2013; Coux *et al.*, 2016). Likewise, the identity of the most important pollinators is not fixed and might vary over time (Brosi and Briggs, 2013). Since the identity of the most efficient and important pollinators will hence vary in space and in time, maintaining high biodiversity can provide an insurance for maintaining pollination services in the face of environmental changes (Brittain, Kremen and Klein, 2013; Kleijn *et al.*, 2015).

1.3 How are plant-pollinator networks assembled?

The structure and assembly of natural communities has offered a long-term conundrum for ecologists. Both abiotic and biotic factors affect the abundance and the distribution of species, and their interactions with each other. The two trophic layers of plant-pollinator networks are assembled through a cross-fire of abiotic, biotic and random processes (e.g. Zobel, 1997; see Fig. 1.). These processes determine which species are present in the global, regional and local species pools. Of these, the global species pool contains all existing species, the regional species pool contains the subset of species in the global pool which able to enter the area, while the local species pool is a subset of the regional species as filtered by environmental conditions as well as by prior presence of suitable interaction partners (Zobel, 1997; Kraft *et al.*, 2012). Finally, the local conditions determine which species are present at a given time in given conditions, and which species could thus potentially interact with each other.

Past events may also have a strong effect on community structure, e.g. through the dispersal history of the regional species pool. In the Arctic, the glaciation history strongly affects the distribution of species and the communities are still recovering from the last glaciation maximum (Hultén, 1937; Hopkins, 1967; Abbott *et al.*, 2000). In Arctic plants, genetic diversity and species richness have been found to be highest close to glaciation refugia, to which species retreated during the glaciation maximum (Eidesen *et al.*, 2013; Stewart *et al.*, 2016). With a warming

climate, species communities followed the retreating ice sheet and thus, modern species and their potential interactions bear signs of this past dispersal history.

On top of the local pool of available species, environmental conditions may strongly shape the structure of the plant-pollinator network (Pellissier *et al.*, 2018). At the finest scale, variation in environmental conditions can affect whether and how an interaction between plants and pollinators species occur. For example, wind speed has been found to change the visitation patterns of pollinators on almond trees. The extent of change was dependent on the diversity of the pollinator communities, suggesting that biodiversity buffers ecosystem functioning under environmental change (Brittain, Kremen and Klein, 2013).

As the environment has a strong effect on community structure, man-induced change, e.g. climate warming and fragmentation, is likely to have an increasing impact. This impact is not solely limited to the loss of species and potential interaction partners, but changing environmental conditions may also reshape interaction structure among remaining species. With changes in the set of species and the interactions realized between them, the functioning of ecosystems and the provisioning of ecosystem services will also be challenged.

1.4. Global change causes loss of biodiversity and ecosystem functioning

Mankind is affecting the ecosystems worldwide. Hence, land-use changes, fragmentation of habitats and climate warming are recognized as the main drivers to current loss of biodiversity (e.g. Tilman *et al.*, 1994; Thomas *et al.*, 2004). Given that high biodiversity promotes efficient ecosystem functioning, we might be facing major changes in the functioning of ecosystems. Thus, the loss of biodiversity is considered one of the largest crises faced by humanity (Heywood, 1992).

On top of decline in biodiversity in general, the biodiversity and abundance of insects, including most of the pollinators, have been observed to decline, especially in industrialized countries (Biesmeijer *et al.*, 2006; Pettis and Delaplane, 2010; Potts, Biesmeijer, *et al.*, 2010; Burkle, Marlin and Knight, 2013; Carvalheiro *et al.*, 2013; Hallmann *et al.*, 2017). This decline of pollinators and pollination services is not limited to natural pollinator communities, but likewise applies to both natural and domesticated pollinators (e.g. Watanabe, 1994; Cox-Foster, Conlan and Holmes, 2007; Bromenshenk, Henderson and Wick, 2010; Pettis and Delaplane, 2010).

Climate change, intensification of land-use, fragmentation of habitats, invasive species, pesticides and pathogens are the main threats to pollinators, as well as to the ecosystem services that they provide (Potts, Roberts, *et al.*, 2010; Carvalheiro *et al.*, 2013; González-Varo *et al.*, 2013; Vanbergen, 2013; Hoiss, Krauss and Steffan-Dewenter, 2015). In many environments, several of these threats are present simultaneously (González-Varo *et al.*, 2013; Vanbergen, 2013), and their combined effects challenge the stability of pollinator communities. Given the important role of pollinators in the ecosystems and in crop production, the current decline of pollinators come with potentially devastating consequences, such as a significant decline in crop production (Packer and Owen, 2001; Gallai *et al.*, 2009).

The functional traits of plants and pollinators affect their vulnerability to changes. The length of the flight season, dietary flexibility and body size are among the most important aspects in explaining pollinator distribution patterns (Bommarco *et al.*, 2010; Bartomeus *et al.*, 2013; De Palma *et al.*, 2015). Species with shorter flight season are less abundant on cropland areas – apparently because a short flight season can easily be desynchronized with floral resources in areas of low plant diversity (De Palma *et al.*, 2015). Among plants, perennial and pollination-demanding species have declined under land-use intensification, whereas many annual plants actually do better in unstable habitats (Moser *et al.*, 2015). Under intensive cultivation and efficient land use, the proportion of outcrossing plant species decreases while the amount of self-pollinated plant species increases (Moser *et al.*, 2015). All these changes affecting the populations of plant species may in turn have a cascading effects on species with which they interact (Miller-Rushing *et al.*, 2010; Evans, Pocock and Memmott, 2013). In the extreme case, the extinction of a species will cause the extinction of its interaction partners (Memmott, Waser and Price, 2004).

Man-induced changes in habitats will affect the performance of individual species differently, causing some species to decrease whereas others might increase (Brittain, Kremen and Klein, 2013). Meanwhile, local extinctions as well as effects of invasive species increase (Clavero and García-Berthou, 2005; Kuussaari *et al.*, 2009). Altering species composition will also modify plant-pollinator interactions and the large-scale structures of

their interaction networks (Bartomeus, Vilà and Santamaría, 2008; Thébault and Fontaine, 2010; Stavert *et al.*, 2018). When the structure of the network changes, both direct and indirect effects may arise, the latter of which are mediated by interaction partners (Holt, 1977; Faeth, 1986; Wootton, 1994; Roslin *et al.*, 2013; Miller *et al.*, 2015; Simmons *et al.*, 2018).

The most connected and abundant species are generally most resistant to changes in the structures of the interaction networks (Dunne, Williams and Martinez, 2002; Verdú and Valiente-Banuet, 2008; Winfree *et al.*, 2014). These core species are the ones maintaining the stability of mutualistic communities (May, 1976; Dunne, Williams and Martinez, 2002; Memmott, Waser and Price, 2004; Montoya, Pimm and Solé, 2006; Verdú and Valiente-Banuet, 2008; Kaiser-Bunbury *et al.*, 2010; Thébault and Fontaine, 2010; Cardinale *et al.*, 2012). In simulations, it has been found that if these most abundant and well-connected species are lost, then the whole community is prone to secondary loss of species (Fortuna and Bascompte, 2006). In general, simulated pollination communities have been shown to be robust to the loss of pollinator species, whereas empirical data partly suggest the opposite: Removing a single, though abundant, pollinator species from a community caused the visitation patterns of the remaining pollinators to change (Brosi and Briggs, 2013). This removal of a single species also decreased the fidelity of other pollinator species to flower species, thus launching a potential cascading effect on the pollination efficiency at the community level (Brosi and Briggs, 2013).

In conclusion, an accurate description of interaction networks is essential for predicting how they will function under environmental change. Networks of plants and their pollinators are known to be resilient and could adjust to the environmental changes. Even though our understanding on how networks are structured and function has improved, much uncertainty remains in terms of what will happen to the network structures and functioning in changing environments. Understanding the effects of a loss of diversity on associated ecosystem services is of greatest interest given current man-induced changes to communities worldwide.

1.5. The species-poor Arctic offers a good model system for understanding plant-pollinator interactions

In general, biodiversity decreases with increasing latitude (Pianka, 1966; MacArthur, 1972). As both the Arctic fauna and flora are species poor (e.g. Lundgren and Olesen, 2005), the plant-pollinator networks of the Arctic are also simple and tractable (Pianka, 1966; Olesen and Jordano, 2002). In addition, arctic plants and pollinators are tightly connected, since most of the Arctic insect fauna visits flowers (Hocking, 1968; Lundgren and Olesen, 2005) and many of the flowers require insects for optimal seed set (Kevan, 1972). In addition to pollen and nectar, Arctic pollinators search for shelter in the flowers, which have been found to offer microclimatic hotspots warmer than the environment (Kevan, 1972; Dietrich and Körner, 2014).

Since the structure of natural interaction networks tends to be extremely complex (Fontaine *et al.*, 2011; Evans, Pocock and Memmott, 2013), the species-poor Arctic provides a convenient model system for understanding the links between the structure and functioning of networks. Additionally, the short summers force both plants and flower-visiting insects to reproduce rapidly after the snow-melt before winter returns. Thus, the combination of a short snow-free period with limited species number facilitates the task of sampling the full seasonal span of spatial and temporal variation in species communities, and of tying their structure to seasonal patterns in ecosystem functioning.

1.6. Arctic pollination and the warming climate

The Arctic is changing fast, and the effects of global warming are especially pronounced in this area. Overall, the pace of temperature increase is twice faster in this region as compared to the global average (Kattsov *et al.*, 2015). Thus, one may expect major climatic impacts on the arctic ecosystems in the near future. In fact, many changes can already be detected: the snow-free area (Tedesco *et al.*, 2011) and the shrub cover (Sturm *et al.*, 2001) are increasing, and interactions between plants and pollinators are challenged by shifting phenologies (Schmidt *et al.*, 2016) and by pollinator declines (Loboda *et al.*, 2017).

Bees (Apoidea) are considered as the most important pollinators worldwide, but they are missing from the northernmost areas. This lack of bees contributes to making muscid flies (Muscidae) the most important pollinators in many Arctic and alpine areas (McAlpine, 1965; Kevan, 1972; Pont, 1993; Elberling and Olesen, 1999). At Zackenberg, North East Greenland, the amount of muscid flies has decreased by a devastating 80% during the past two decades (Loboda *et al.*, 2017). Such loss of

efficient pollinators is likely to affect the pollination and seed set of the plants (Kaiser-Bunbury *et al.*, 2010).

Seasonal patterns in the abundance of insects in the Alpine and Arctic depends strongly on temperature (Totland, 1994; Hodkinson and Coulson, 2004; Høye, Ellebjerg and Philipp, 2007) and on snow-melt (Nielsen and Schmidt, 2013; Loboda *et al.*, 2017; Kankaanpää *et al.*, 2018). Likewise, the flowering phenology of arctic plants is strongly affected by the accumulation of degree days (Thórhallsdóttir, 1998; Høye, Ellebjerg and Philipp, 2007) and by snow-melt (Høye, Ellebjerg and Philipp, 2007). As a result, the warming climate affects the phenology of arctic species at both trophic levels, and interactions between plants and their visitors have to adjust to this (Hodkinson *et al.*, 1998; Miller-Rushing *et al.*, 2010; Høye *et al.*, 2013).

In general, spring has become earlier in Greenland (Høye *et al.*, 2007, 2013) while the phenologies of insects and plants have shifted in idiosyncratic manners (Schmidt *et al.*, 2016). However, for pollination to happen, these two guilds need to meet in time (Burkle and Alarcón, 2011), and any temporal mismatch may hamper pollination (Hegland *et al.*, 2009; Miller-Rushing *et al.*, 2010; Schmidt *et al.*, 2016). That such challenges are currently occurring was suggested by the observation of an increased mismatch between plant flowering and pollinators in NE Greenland (Høye *et al.*, 2013; Schmidt *et al.*, 2016). Such a mismatch may prove particularly harmful in the short arctic summer where a lack of time after flowering and pollination may result in reproductive failure (Thórhallsdóttir, 1998). A temporal mismatch might thus lead to flowers without pollinators and pollinators without nectar and pollen (Høye *et al.*, 2013; Schmidt *et al.*, 2016).

On top of climate warming, inter-annual fluctuations in environmental conditions, such as snow-cover, temperature and weather in general, are challenging arctic pollination (Schmidt *et al.*, 2016; Kankaanpää *et al.*, 2018). The arctic pollination is highly weather-dependent as the activity of insect pollinators depends on the temperature and sunshine; the pollinators are not moving if the weather is bad (McAlpine, 1965; Kevan and Baker, 1983; Totland, 1994; Hodkinson, Coulson and Webb, 1996; Høye and Forchhammer, 2008; Wheeler *et al.*, 2015). Poor weather conditions might also affect the plants' ability to get pollinated and produce seeds (Wada, 1999). When the climate is warming, the springs become earlier, and the probability of extreme weather events (e.g. severe frost) during flowering increase (Wheeler *et al.*, 2015). This could lead to failure in the reproduction of both plants and insects.

As the effects of climate warming and inter-annual fluctuations in environmental conditions become stronger in the Arctic, and since biodiversity in general enhances ecosystem robustness (Dunne, Williams and Martinez, 2002; Kaiser-Bunbury *et al.*, 2010), the species-poor arctic systems are likely to be vulnerable to ongoing change. However, the fact that major fluctuations are natural parts of the Arctic climate, and that species are hence adapted to such variation (Scholander *et al.*, 1950; Bliss. L and Bliss, 1962; Addo-Bediako, Chown and Gaston, 2002), may dampen some of the short-term impacts at the ecosystem level. Nonetheless, individual species may still be strongly affected by the changes (Hodkinson *et al.*, 1998; Post *et al.*, 2009).

1.7. Aim of the thesis

To address links between the biodiversity and ecosystem functioning in interaction networks, I studied pollination at a High Arctic site – the Zackenberg valley in North East Greenland (**I** & **III**). To acquire a pan-arctic perspective on pollination networks, I complemented my work at Zackenberg with a study spanning a wide range of latitudes. To this aim, I analyzed the local pollinator assemblage and plant seed set at 15 locations spread across the Arctic (**II**). Overall, I asked the following questions:

1. Within arctic pollination networks, are some of the species, genera or families more important than others? (**I**, **II** & **III**)
2. How does the structure of the flower-visiting community reflect into its functioning? (**I**, **II** & **III**)
3. Are there pan-arctic patterns in the structure of flower-visiting communities and/or in their functioning? (**II**)
4. What seasonal patterns may we distinguish in the structure of arctic pollination networks and in relation to ecosystem functioning? (**I** & **III**)
5. How will climate change affect the pollination service in the High Arctic? (**I**, **II** & **III**)

How the different chapters of my thesis relate to the overall framework of community assembly, and how they link to each other is visualized in Figure 1.

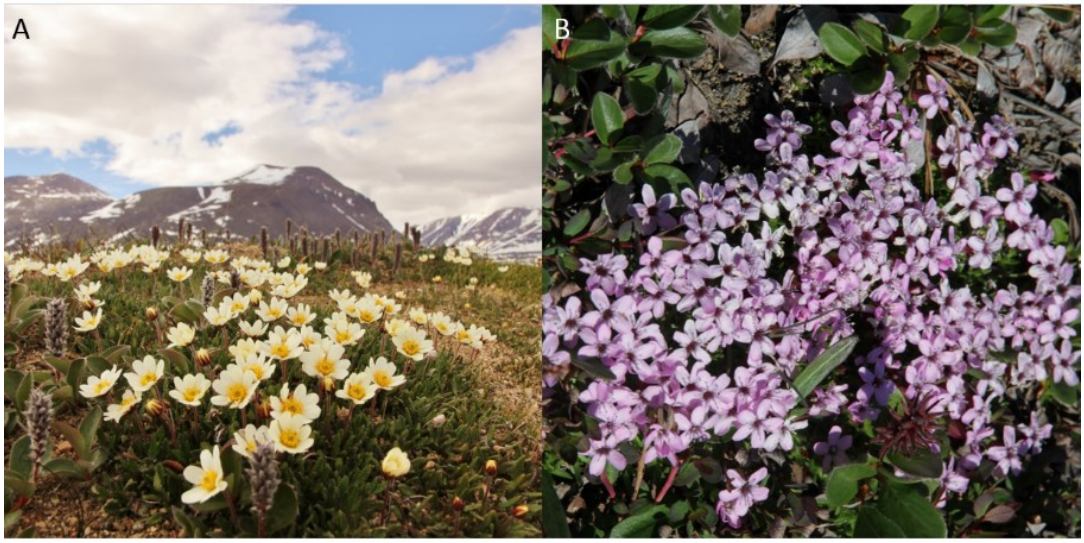

Figure 2. Key species addressed in my study: A) *Dryas* and B) *Silene acaulis*. Panel A shows a *Dryas* tussock growing at Zackenberg, North East Greenland. In this region, most individuals of Avens are hybrids *Dryas octopetala×integrifolia* (Philipp and Siegismund, 2003).

2. METHODS

My study focuses on the pollination networks of the Arctic, and especially on the communities related to the wide-spread Avens, *Dryas* sp. (Rosaceae, see Fig. 2A). This is one of the most important flowering plants in the High Artic (Lundgren and Olesen, 2005; Rasmussen *et al.*, 2013). I conducted the work related to Chapters **I** & **III** in the Zackenberg valley (74°30' N, 21°00' W, for detailed locations see Figures 3A & 4A) in the North-East Greenland national park. The valley is characterized by a High Arctic climate, with monthly average temperatures ranging from -20 to 7 °C and annual precipitation being around 260 mm (Sigsgaard *et al.*, 2008). The landscape is mainly covered by small shrubs and erosion by water and ice creates many vegetation-free patches of mineral soil and the vegetation of the valley is a diverse mosaic (Bay, 1998), creating pronounced spatial variation in assemblage structure of the local flower visitors.

The Zackenberg site is characterized by a relatively simple species community (Wirta *et al.*, 2014), and yet it has all the essential layers of a traditional trophic network (see Schmidt *et al.*, 2016). The lack of massive number of species in this specific network allows us to look the roles of individual species or species groups in more detail.

To address whether some of the species, genera or families more important than others within arctic pollination networks, I sampled flower-visitors with sticky traps mimicking *Dryas*-flowers (**I** & **II**, for study design see Fig. 3B). To track broader patterns in the Arctic pollination networks and in their functioning, I used a distributed study design, where simple-to-use sampling kits were sent to 15 research stations across the northern hemisphere (see Fig. 5).

Given the large geographical and taxonomical span of my flower-visitor samples, all the pollinators caught in Chapters **I** & **II** were identified with DNA-based methods – replacing the need for extensive, time- and resource-consuming involvement of taxonomic experts around the world. The identification of individuals was based on the DNA barcode region of mitochondrial cytochrome c oxidase 1 (CO1), as routinely used in identification of animals (Hebert *et al.*, 2003). The DNA was extracted from a small tissue sample of each individual caught, and the samples were PCR-amplified and sequenced in the Canadian Center for DNA Barcoding following their standard protocols (CCDB, www.ccdb.ca/resources.php). The sequence information was then imported to Barcode of Life Data Systems (BOLD, www.barcodinglife.org (Ratnasingham and Hebert, 2007)) to be compared and identified with the reference barcodes. In my thesis, I use barcode index numbers (BINs; Ratnasingham and Hebert, 2013) as taxonomical units – since with few exceptions, a BIN equals a morphologically identifiable species (Wirta *et al.*, 2016).

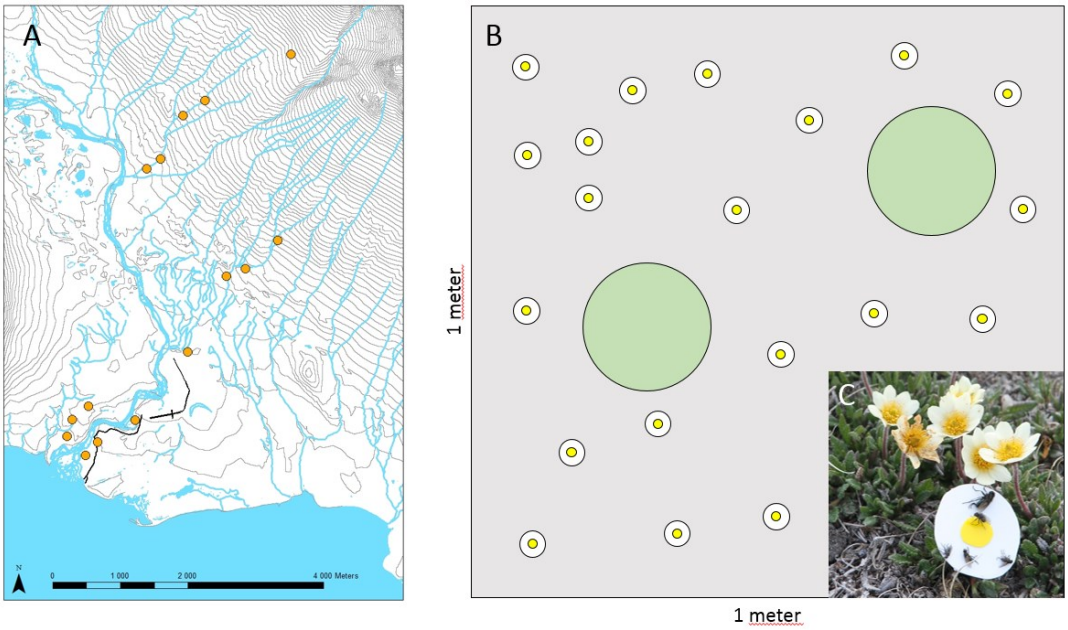

Figure 3. Locations (A) of the study sites in Chapter **I** and design (B) of the study sites in Chapters **I** & **II,** with a photography of a sticky flower mimic (C) used to sample insects. In panel A, the yellow circles represent the locations of the study sites within the Zackenberg valley in northeastern Greenland. In panel B, the white circles with yellow center represent the 20 sticky traps placed in each of the study squares. The sticky traps shown in C were installed for three days during the peak flowering of *Dryas*. The light green circles represent the pollinator exclusion cages (Ø 20 cm). To resolve the effect of flower visitors, the seed set of *Dryas* was recorded separately for the flowers inside and outside the exclusions in the end of the season. Five similar study squares were established at each of the study sites.

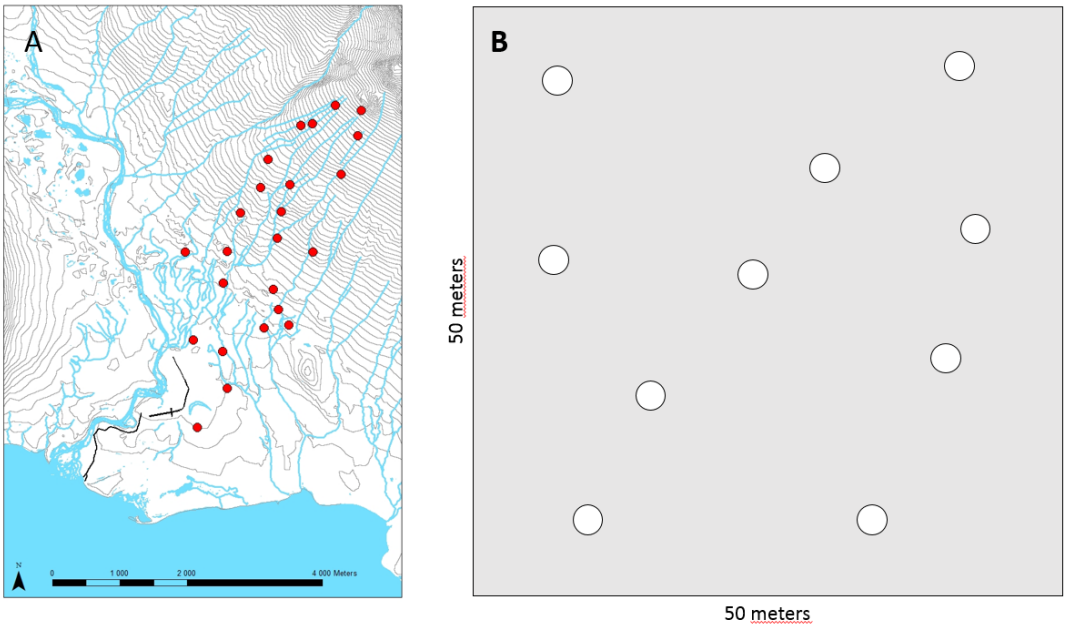

Figure 4. Locations (A) and design (B) of the study sites in Chapter III. In panel A, the red circles represent the locations of the study sites within the Zackenberg valley in northeastern Greenland. In the panel B, the empty circles represent the ten study plots within each study site. The overall flower abundance, pollen loads on muscid flies and seed set of flowers was recorded at the level of these individual study sites. In addition, flower abundance and visitation rates on flowers were recorded at the level of the study plot.

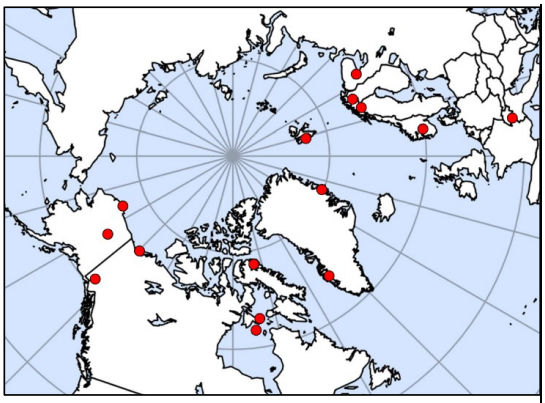

Figure 5. Locations of the study sites of Chapter II. The red circles represent the locations of the study sites. The map is adapted from Chen-Pan Liao, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=14530212.

How the structure of the flower-visiting community reflect into its functioning was examined by monitoring especially *Dryas* (**I** & **II**) but also other plant species (**III**). Here, I used seed set as a key measure of ecosystem functioning, and related this metric of pollination success to the structure of the flower-visiting community observed at the same sites. Since we used *Dryas*-mimicking sticky traps, we recorded only the seed set of *Dryas* in Chapters **I** & **II**. Scoring of seed set was based on recording what fraction of flowers had produced seed heads at the end of the growing season. To separate effects of pollinators from seed set by autogamy, we used small cages to exclude pollinators from some of the flowers.

To track seasonal patterns in the structure of arctic pollination networks and in relation to ecosystem functioning, I recorded season-long spatial patterns in the pollination network and in its functioning at Zackenberg (**III**). To this end, I monitored phenological patterns in flower abundance, pollinator visitation rate and pollen loads carried by muscid flies, and in the seed-set of the most common plant species, at 24 sites followed through the two months of arctic summer (for study site locations and design see Fig. 4B).

To address how climate change affects the pollination service in the High Arctic, I used a space-for-time design to first identify the key contributors to current functioning, then relating variation in this functioning to current variation along environmental gradients (**I**, **II** & **III**). In general, environmental conditions of higher altitudes and latitudes reflect a colder climate, and the effects of climate on communities could thus be seen by comparing patterns at such colder areas to patterns at lower altitudes and elevations (Walker and Mathewes, 1989; Kearns, 1992; Pont, 1993; Elmendorf *et al.*, 2015). Thus, the sampling effort in Chapters **I** & **III** was distributed across 15 and 24 sampling sites, respectively, along an elevational gradient. In Chapter **II**, I sampled pollinator communities across a latitudinal gradient.

3. RESULTS AND DISCUSSION

In this thesis, I found Arctic pollination networks to be highly diverse, but dominated by just a few of the species present. Signs of past glaciation history were found in current community composition, with the highest taxonomic diversity detected in areas closer to past glacial refugia. Regional communities differed substantially in terms of species composition, with surprisingly high β-diversity (i.e. few species shared among sites). The community of flowering plants was highly seasonal and the community of flower-visitors surprisingly diverse. Based on my experiments in Zackenberg, almost the whole insect fauna visits the flowers and could be considered potential pollinators. On top of that, Arctic plants are tightly tied to their pollinators, and seem to suffer from severe pollen limitation (e.g. Ashman *et al.*, 2004), resulting in strong competition for pollination especially during the short flowering peak of the early summer.

Though the pollinator community was relatively abundant and diverse, I found only a small portion of it to be generating most of its functioning. In the plant community, *Dryas* emerged as the dominant species acquiring most of the flower visits, dominating the pollen loads on pollinators and providing a resource for almost the whole local insect fauna. In the insect community, muscid flies proved the key pollinators. They carry loads of pollen between the flowers and the seed set of *Dryas* increases with muscid abundance. By contrast, the diversity of the rest of the flower-visiting community did not detectably effect ecosystem functioning.

At present, the decline of pollinators is not limited to lower latitudes, but is also documented in the very same Arctic community that I have been working with (Zackenberg; Loboda *et al.*, 2017). As climate change is challenging the phenology of interactions which sustain arctic pollination (Schmidt *et al.*, 2016), the future functioning of pollination in arctic ecosystems may be imperiled. My observation of strong competition for

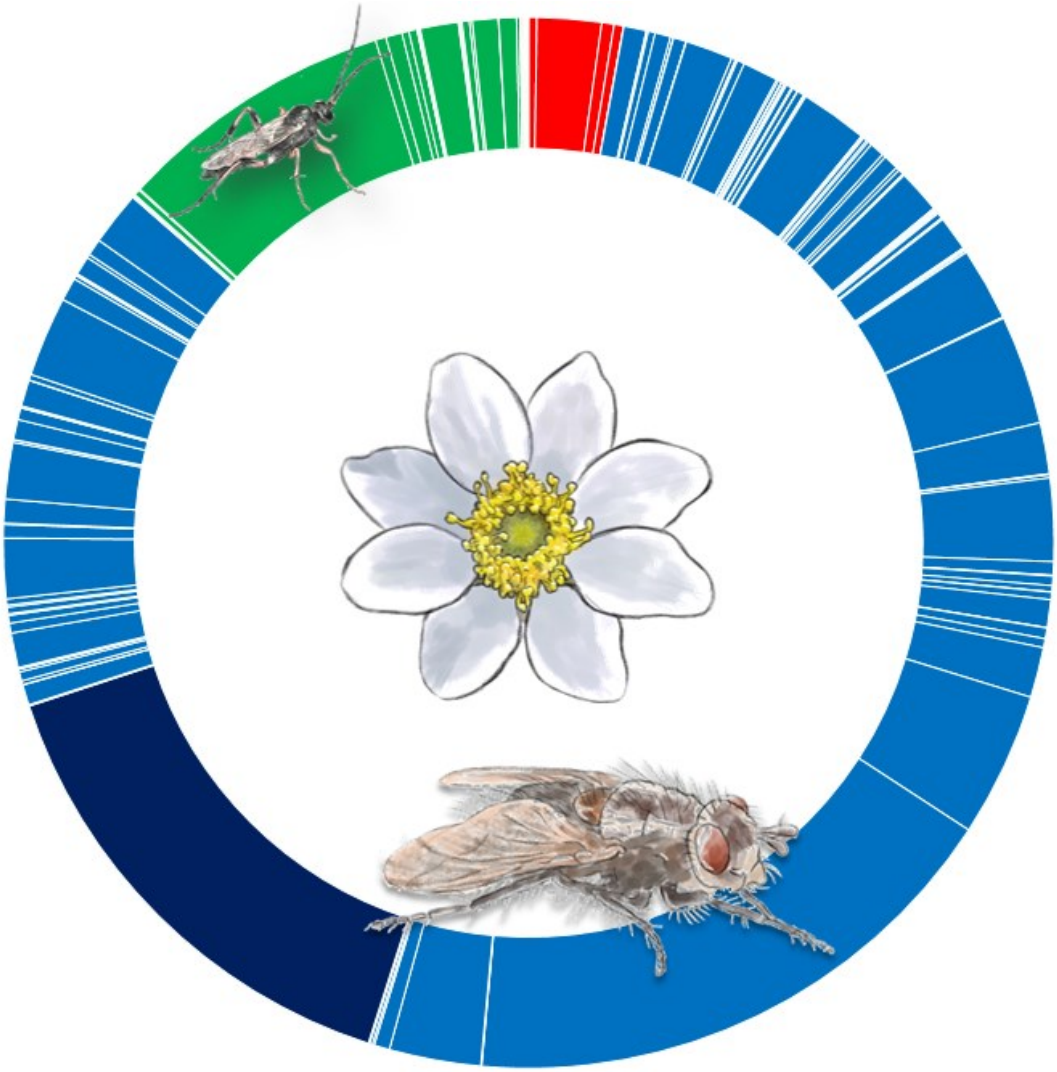

Figure 6. Composition of flower visiting community of Dryas at Zackenberg. The sectors represent individual species caught (n = 180). Red, blue, green and yellow sectors represent Araneae, Diptera, Hymenoptera and Lepidoptera, respectively. The dark blue sector represents the most important pollinator species, Spilogona sanctipauli Muscidae. The width of the sectors indicates the relative proportion of the species. The chart is based on 7,947 individual flower-visitors.

pollinators during the flowering peak may in part be a recent phenomenon, caused by a decline of muscid flies during the last few decades (Loboda et al. 2017) and by a recent plant-pollinator mismatch (Schmidt et al. 2017). If so, the consequences may be aggravated as climate warming continues.

3.1. Within arctic pollination networks, are some of the species, genera or families more important than others?

In general, the Arctic area is species poor and this pattern is also reflected in the structure of arctic pollination networks (e.g. Pianka, 1966; Pont, 1993; Rasmussen *et al.*, 2013). However, across the Arctic we found *Dryas* mimicking sticky traps to attract as many as 26,406 individuals of 1,360 flower visiting species (**II**). Thus, my work reveals a match between the Arctic area and lower latitudes: most insects worldwide are attracted by the nectar and pollen provided by flowers (Olesen and Jordano, 2002; Ollerton, Winfree and Tarrant, 2011). The flower visiting community also emerged as extremely diverse compared to the full fauna previously recorded from the regions sampled. At a smaller scale, at

Zackenberg, intensive sampling with sticky flower-mimics captured more than two-thirds of the full local insect fauna (**I**, Fig. 6). Thus, *Dryas* emerges as a resource uniting the whole insect community.

Based on my results in Chapters **I**, **II** & **III**, the contribution of individual plants and flower-visiting species to the structure and functioning of arctic communities is highly uneven. In terms of both plants and flower-visitors, some species were highly abundant and dominated the network. In Chapter **III**, I tracked the seasonal patterns of the plant community in the Zackenberg valley. Together, the three most abundant flowering species accounted for a full 80.2% of all flowers in the region, with *Cassiope tetragona*, *Dryas octopetala* and *Bistorta vivipara* making up 42.0 %, 31.2 % and 7.4 % of the flowers on my study sites, respectively. While *Dryas* accounted for 56.2% of the flowers on my observational study plots, it alone received more than 97.2% of all flower visits by insects.

Just as the functioning of the plant community was dominated by a few plant species, and by *Dryas* in particular, the flower-visiting insect community was likewise dominated by a few highly abundant species: In Zackenberg, the three most common species accounting for a total of 41.3% of the flower visits were *Drymeia* sp. (Diptera: Muscidae), *Spilogona sanctipauli* and *Microplitis lugubris* (Hymenoptera: Braconidae) attributed for 17.4%, 15.2% and 8.7% of the flower-visits, respectively. This pattern, where majority of the flower visitors trapped at a given site belonged to a relatively small pool of species was similar across the Arctic (**II**), with the three most common flower visitors accounting for an average of 45.3% (±SE15.7%) of all flower-visits.

Spatial variation in the flower-visiting communities of the high Arctic was high at both the local (**I**) and pan-arctic (**II**) scale. Given this variation, no single species or family will dominate the contribution of pollinators across the whole Arctic. High local (α) diversity will then increase the probability that an efficient pollinator will be present within the fauna of a given area. Even though high species turnover (β diversity) at the species level communities, some families, e.g. Chironomidae and Muscidae were relatively abundant (22.6% SE±16.4% and 19.8% SE±8.6%, respectively) across the sampled sites, suggesting an important role for them in all Arctic ecosystems.

As *Dryas* received almost all the flower visits, it is evident that it provides a highly important resource for the flower-visiting insects. This was further shown in Chapter **I**, where I encountered 185 different arthropod species, including two thirds (177/269) of all the insects encountered in Zackenberg (Wirta *et al.*, 2016), on sticky *Dryas*-mimicking traps. Also in the pan-arctic study, *Dryas*-mimics were attracting a wide taxonomic range of flower-visitors.

In conclusion, my results reveal large variation in the composition of flower-visiting communities of the Arctic, but suggest that most of them are dominated by a few locally abundant insect species. While the flower-visitor communities showed no pan-arctic patterns, among the plants, *Dryas* emerges as a widely distributed, locally abundant species, which is visited by a wide range of flower visiting species. Thus, one could say that *Dryas* is truly a key species of the Arctic, tying together the whole pollination network.

3.2. How does the structure of the flower-visiting community reflect into its functioning?

As mentioned above, the abundance of individual plant species was not directly reflected in their functional importance within the pollination network, since *Dryas* attracted practically all the flower-visits. In terms of the pollination of *Dryas*, a single fly family, Muscidae, and even a single species within this family, *Spilogona sanctipauli*, proved the main contributor to seed set at Zackenberg (**I**). Meanwhile, overall species diversity in the pollinator community did not detectably increase ecosystem functioning (*sensu* seed set). In terms of biodiversity effects on ecosystem functioning (sampling vs. complementary hypothesis; Loreau *et al.*, 2001; Tilman *et al.*, 2001; Cardinale, Palmer and Collins, 2002; Hooper, Chapin and Ewel, 2005), my results are consistent with the sampling hypothesis, where a few important species or species groups sustain most of the pollination function.

In Chapter **III**, I observed patterns of intra- and interspecific competition for pollination among the plants of the High Arctic. Since muscid flies appeared the most important pollinators at Zackenberg (**I**), I was interested in their pollen carrying abilities and thus monitored their pollen loads in Chapter **III**. Here, the relatively abundant muscid flies emerged as truly efficient pollinators, carrying an average of 260 pollen grains per individual, as compared to lower counts in other taxa of the area (Nielsen and Schmidt, 2013). Among the plants, *Dryas* again transpired as the dominant species, contributing 90.4% of all pollen grains carried by muscid flies.

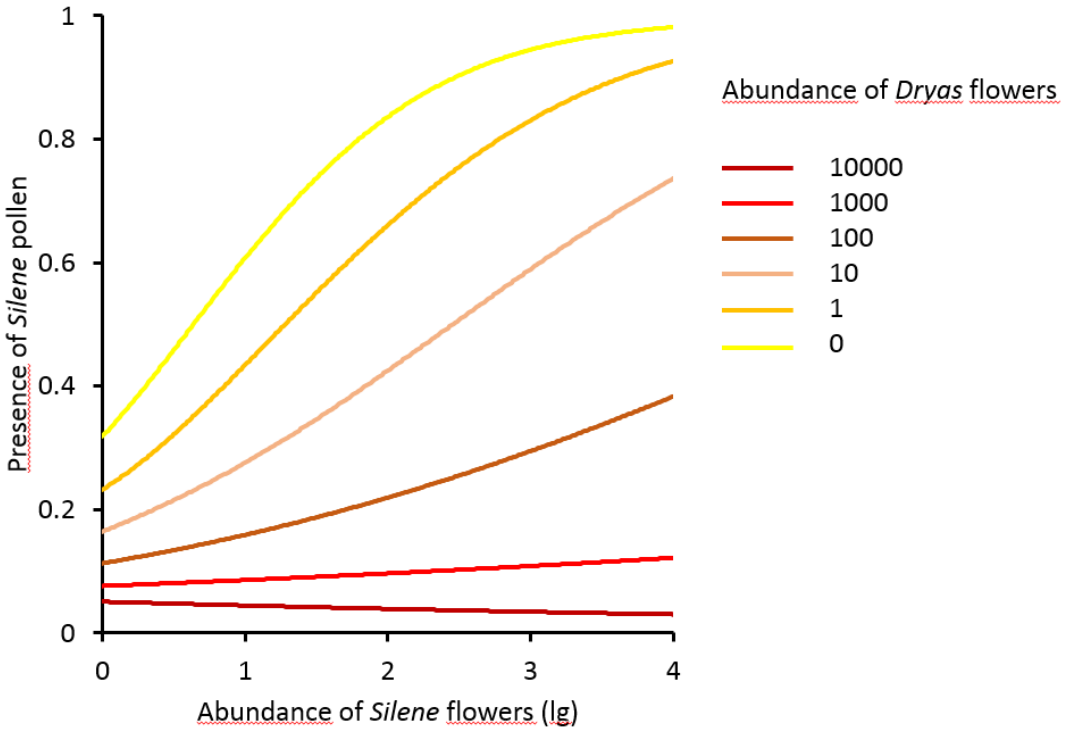

Figure 7. Presence of Silene pollen on muscid flies as a function of Silene and Dryas flower abundances recorded at the study sites. The y-axis shows the probability with which Silene pollen was found on individual muscid flies, while the x-axis shows log10(a+1)-transformed Silene flower abundance. Lines of different colors represent different abundances of Dryas flowers. The graph shows fitted probabilities from the GLMM described in the Chapter III.

Competition resulting from the high abundance of *Dryas* flowers was visible not only in reduced visitation rates on other flowering species (see above), but was also evident in the pollen loads and seed set of plants. While an increasing abundance of *Silene acaulis* (Caryophyllaceae, Fig. 2B) flowers increased the presence of *Silene* pollen on muscid flies, an increasing abundance of *Dryas* flowers cancelled out this effect, weakening the relationship between *Silene* flower abundance and *Silene* pollen transport (see, Fig. 7). In terms of seed set, high abundances of *Dryas* flowers during the flowering of *Silene* and *Dryas* individuals resulted in decreased seed set by both species.

As such, the *inter*specific competition observed in the pollen loads and seed set between a dominant plant (*Dryas*) and a sympatric taxon (*Silene*) was perhaps no surprise, but such effects have rarely been documented in nature. *Intra*specific competition for pollination, as observed in the seed set of *Dryas*, was perhaps more surprising. Past studies have suggested that a high amount of conspecific flowers may rather promote more efficient pollination through decreased amount of heterospecific visits and pollen deposition (Blüthgen *et al.*, 2007; King, Ballantyne and Willmer, 2013; Ballantyne, Baldock and Willmer, 2015). However, my findings suggest that pollinator abundance may sometimes fall short of fulfilling the pollination need by the plants – in particular during strong bouts of flowering during the short summer of the High Arctic.

While *Dryas* attracts a large portion of the flower-visiting insects available, it still seems strongly pollen and pollinator limited. At all spatial scales, the presence of pollinators increased the seed set of *Dryas*. Such effects were found both within the Zackenberg valley and across the Arctic, with a 24.7% ±SE11.7% and 30.3% ±SE22.5% increase in seed set, respectively, recorded in the presence of flower-visitors (**I** & **II**). Even in the presence of pollinators, pollen limitation remained evident at both the local scale and the pan-arctic scales, as only 33.6% (±SE12.6%) and 53.0% (±SE19.0%) of the seed heads were

producing seeds, respectively. This pollination limitation was evident and became more severe during the peak flowering of *Dryas*, as the seed set of both *Dryas* and *Silene* decreased with high *Dryas* densities in Chapter **III**.

While Arctic pollination communities are dominated by a few plant and flower-visiting species, such dominance can also be found at the lower latitudes. E.g. the pollination networks of agricultural habitats are similarly dominated by only few species (e.g. Goodwin, Cox and Taylor, 2011; Rucker and Thurman, 2012; Kleijn *et al.*, 2015), and invasive plants are also dominating the pollination networks of some areas (Brown, Mitchell and Graham, 2002; Clavero and García-Berthou, 2005; Bartomeus, Vilà and Santamaría, 2008). If this dominance reflects into the functioning of the network as it does in the Arctic, then one may expect matching effects in agricultural systems: A farmer may then want to monitor that the crop plant receives enough flower visits not to suffer from pollen limitation and/or intraspecific competition. In addition, from the perspective of natural plants, pollination competition with crop plants may be causing reduced offspring and hamper the population. Even though crop plants are believed to have only minor effects on natural plant communities (Magrach *et al.*, 2018), crop plant flowering may still reduce reproductive performance to a so far unknown extent. Thus, my findings from an arctic plant in the furthest North (*Silene* at Zackenberg) offer some cause of concern for communities at other latitudes, as dominated by abundant crop species and other invasive species.

3.3. Are there pan-arctic patterns in the structure of pollinator communities and/or in their functioning?

In my comparison of flower-visitors across the Arctic (**II**), I found large site-to-site variation in the structure and composition of the pollinator community. The seed set of *Dryas*, recorded as a measure of ecosystem functioning, likewise showed large variation between sites. By linking species richness and environmental conditions, I was able to show that the local flower-visitor communities were shaped by temperature and precipitation. Both local precipitation and temperature emerged as key predictors of local flower-visitor diversity. In addition, the structure of flower-visitor communities and their phylogenetic diversity seemed related to the glaciation history of the region, being highest close to past glaciation refugia. While at Zackenberg, muscid flies were identified as the most important pollinators of *Dryas* (**I**), no similar pattern emerged at the an-arctic scale. Here, variation in community structure, environmental factors and the levels of autogamy of *Dryas* strains all varied in idiosyncratic manners (Fig. 8).

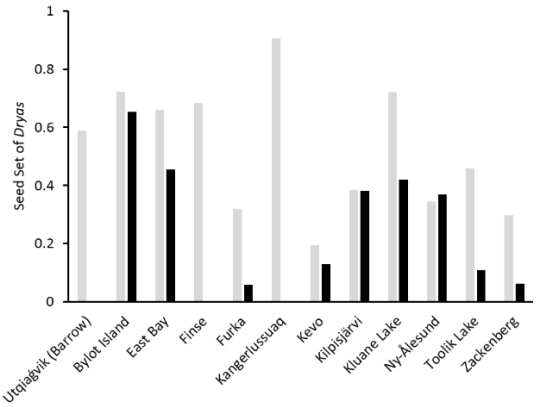

Figure 8. Seed set of Dryas at individual sites. The y-axis shows the proportion of successful seed set in Dryas. Light gray and black bars represent seed set with pollinators present versus excluded, respectively. Exclusions were not used in Finse and Kangerlussuaq, whereas at Utqiaġvik (Point Barrow) no seeds were produced in the exclusions.

In terms of the phylogenetic structure of the communities, the largest differences were found between northeastern and northwestern parts of the North America. Surprisingly, this difference was larger than the one between Alaskan and Eurasian communities. These patterns potentially derive from strong glacial isolation between eastern and western North America during the latest glacial periods. The communities of Eurasia and northwest America were similar, as likely reflecting a shared glaciation refugium in Beringia (Hopkins, 1967; Cook *et al.*, 2005; Ávila-Jiménez and Coulson, 2011; Eidesen *et al.*, 2013). Also, the highest phylogenetic diversity among the communities sampled was found at sites near Beringia, adding evidence for an important glaciation refugium in this area.

The structure of flower-visiting communities varied substantially among arctic sites (**II**), resulting in high species turnover (high β-diversity) among sites. With respect to the species shared among sites, European and Alaskan communities (including Zackenberg in North-East Greenland) formed the most distinct groups and shared more species with each other than with northeastern America – a pattern reminiscent of that found for phylogenetic diversity (above). The flower-visiting community of Svalbard shared some species with the community of Zackenberg, likely reflecting the (relative) ease of insect dispersal among these sites. Importantly,

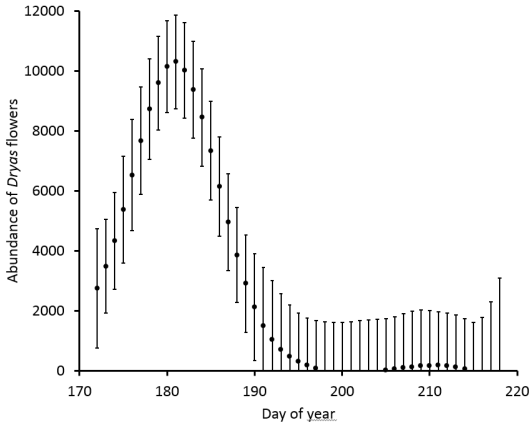

Figure 9. Phenology of Dryas flowering on my study sites in Zackenberg in 2016 (III). The graph shows fitted values from Generalized Additive Mixed Model with the abundance of Dryas flowers as a function of days since January 1 (Day of Year). In the model, the identity of the study site is used as a random effect and day of the year as a smoother. The y-axis shows the predicted abundance of Dryas flowers on a study site, while the x-axis represents the day of the year. The error bars represent 95% -confidence intervals derived from the model.

the patterns observed here for flower-visiting insects were similar to those previously reported from arctic plants (Eidesen *et al.*, 2013; Stewart *et al.*, 2016). This suggests a shared post-glacial dispersal history for both trophic layers in arctic pollination networks.

Given the high number of flower-visitors trapped with the *Dryas*-mimicking traps across a wide geographical range, *Dryas* is highly important for the flower-visitors across the Arctic. In terms of the rates of the ecosystem functioning measured (seed set of *Dryas*), the pan-arctic study revealed great site-to-site variation in levels of seed set in general, and in particular in the level of the seed set contributed by the flower-visiting community. In conclusion, given the high spatial variation in flower-visiting communities and the phenotypical plasticity in *Dryas*, the identity and relative contribution of flower-visitors important to *Dryas* is likely to vary substantially between the regions. This idiosyncratic variation in the structure of flower-visiting communities and in the level of seed set by *Dryas* suggests that the drivers of pollination and seed set will differ among regions.

Overall, the combination of 1) a lack of any detectable relation between species richness and ecosystem functioning at both the local and pan-arctic scale, 2) the existence of a single, functionally dominant pollinator species in one region (**I**, *Spilogona sanctipauli* in Zackenberg), and 3) the occurrence of high β-diversity at a pan-arctic scale uncovered in my thesis work, suggests that the pollination function is provided by different species in different regions. Given high inter-annual variation in arctic communities, these observations support the sampling hypothesis as a plausible explanation for a positive relationship between diversity and ecosystem functioning. Under this scenario, high species richness increases the chances that a particularly efficient pollinator will be present at a given time in a given place.

3.4. What seasonal patterns may we distinguish in the structure of arctic pollination networks and in relation to ecosystem functioning?

Given the shortness of arctic summers, arctic communities exhibit extreme phenological change. The phenology of both plants and flower-visitors is clearly seasonal (**III**), which is common in the arctic and alpine areas (Totland, 1994; Hirao *et al.*, 2006; Mizunaga and Kudo, 2017). At Zackenberg, the flowering proceeds at a quick pace, with the first flowers opening right after the snow-melt. In terms of the pollination network of the high arctic, the most pronounced seasonal pattern was the short peak in flower abundance during the early season (**III**). The flowering of most plant species is concentrated to the early season, with peak abundances reached in the late June and early July (with an average around July 2nd for my study sites). After the flush flowering of the early season, the overall flower abundance drops drastically towards the end of the season. As described in previous sections, the flowering of *Dryas* plays a key role in terms of the functioning of the whole pollination network and ecosystem. At Zackenberg, the flowering peak of *Dryas* is reached at June 30th (Fig. 9), and translates into strong seasonal patterns in the functioning of the overall pollination network.

High seasonal variation in the abundance of flowers resulted in uneven competition for pollinators during different parts of the summer. As a likely result of competition for pollinators, the seed set of plants was highest among flowers open either before (*Dryas*) or after (*Silene*) peak flowering. The overall visitation rate (visits per flower) was highest early in the season, before the flowering peak, as likely due to less flowers competing for the pollinators. Visitation rates then decreased towards the later parts of the season, during and after the flowering peak of *Dryas*. During the highest flowering

peak, the attractive *Dryas* flowers strongly competed for the pollinators with other species (interspecific competition) but also with other individuals of *Dryas* (intraspecific competition). This competition over pollination resulted in a seasonal patterns in the seed set of *Dryas* and *Silene*: the seed set of *Dryas* increased and the seed set of *Silene* decreased with increasing day of year. *Dryas* flowers were producing more seeds early in the season whereas the seed set of *Silene* reached its maximum after the flowering peak. Thus, in terms of seed set, both species perform better outside the highest flowering peak, which was also the peak of competition for the pollination service.

Dryas flower density seems the main reason for competition among plants for pollination in Zackenberg. Indeed, its impact was evident in terms of each response examined: flower visitation rates, pollen loads and seed set. Increased *Dryas* flower densities during peak flowering causes increased pollen limitation and intra- and interspecific competition over the pollination. In Chapter **I**, the sampling of flower visitors with sticky traps was repeated at some of the sites later in the season. For practically all insect species and groups, I found significantly more insects in terms of overall abundance and species richness. Based on this late season sampling, the abundance and diversity of pollinators thus reach their maximum level after the flowering peak of the plants, and their life cycles are likely timed by different cues than is plant flowering. The increased flower visitor abundance after the flowering peak observed may reflect the increasing temporal mismatch of these two guilds observed in Zackenberg (Schmidt *et al.*, 2016). Meanwhile, the observed high level of intra- and intraspecific competition is likely a combined result of this phenological mismatch (Schmidt *et al.*, 2016) and of a decline in populations of the most important pollinators of the region (Loboda *et al.*, 2017).

Overall, the highest abundance of most arctic flowers is concentrated to the flush flowering of the early season. This high seasonality in the pollination network accounted for many of the patterns detected in terms of competition for pollination and in the ecosystem functions driven by flower-visiting insects. To the best of my knowledge, this kind of pollinator-mediated seasonal competition patterns in the seed set of plants has not been previously documented. Yet, patterns similar to the ones here observed for *Dryas* flowering are likely found in other pollination networks dominated by few species, e.g. in agricultural landscapes as well as in ecosystems dominated by invasive species. Increased competition during a short period of intense crop flowering might then result in decreased pollination of both the crop plant itself as well as of wild plants in surrounding habitats (see previous section). This could lead to decreased fitness of species or individuals the flowering of which coincides with the flowering peak of the crops (as was the case for *Dryas* and *Silene* individuals flowering during the flowering peak of *Dryas*).

3.5. How will climate change affect the pollination service in the High Arctic?

The arctic climate is warming twice as fast as the world on average (Kattsov *et al.*, 2015). Even though the Arctic is and has been under constant change with fluctuations in the extent of continental glaciers (Paillard, 1998), and while the region is still recovering from the last glaciation maximum, the changes caused by the warming of the past few decades are already visible (e.g. Sturm *et al.*, 2001; Kattsov *et al.*, 2015; Schmidt *et al.*, 2016). Even though I did not directly monitor the change in the environment and communities between years in my thesis, I did gain snapshots of tens of current pollination networks in my time-for-space study designs along altitudinal (**I** & **III**) or latitudinal gradients (**II**). This gives me an opportunity to speculate about the future functioning of the pollination network under changing environmental conditions and global warming.

In Chapter **III**, the flowering community showed some significant patterns across the elevation gradient. In general, the abundance of flowers decreased with increasing elevation. This pattern was partly caused by a drastic decreased in abundance of some relatively abundant flowering species (e.g. *Cassiope tetragona* Ericacea*, Vaccinium uliginosum* Ericacea) with increasing elevation. Indeed, both *Cassiope* and *Vaccinium* were completely missing from the highest elevations. The highest plant species richness was achieved in intermediate elevations. In Chapter **III**, I also found a relative shift in flowering phenology of *Dryas* and *Silene* along the altitudinal gradient: at higher elevations, *Silene* was flowering earlier compared to the flowering of *Dryas*.

In Chapter **I**, the increasing elevation resulted in decreased seed set by *Dryas*. However, this effect on ecosystem functioning was not likely attributable to changes in the pollinator communities but rather to the environmental conditions, since the effect of elevation

was similar in both flowers with pollinators and flowers from which the pollinators were excluded. Shifts in the plant communities and their phenology, as well as in seed set of *Dryas*, were evident along the elevational gradient, but whether these patterns are attributable to the changes in flower visiting community remains a moot point.

As the timing of flowering of plants and emergence of pollinators are mediated by partly different cues (Gillespie, Baggesen and Cooper, 2016), environmental conditions will likely affect their temporal overlap. Thus, in my study area at Zackenberg, the competitive environment caused by the flowering peak of *Dryas* should be different along the environmental gradients, as the overlap between the flowering peak of plants and the flight season of pollinators varies. Indeed, I found *Silene* flowers at higher elevations to open earlier in relation to the timing of *Dryas* flowering. In conclusion, the functioning of pollination networks is likely challenged by changes in competitive environment, as a result of different phenological responses of plant and pollinator species to climate warming.

The pollen limitation and competition for pollination observed at Zackenberg might actually be due to recent climate change, and may have emerged quite recently in the ecosystem: Over the past two decades, the abundance of the most important pollinators (muscid flies) have declined by 80% (Loboda *et al.*, 2017), and at the same time pollinators and flowers seem to be drifting apart in terms of phenology (Schmidt *et al.*, 2016). Thus, some decades ago, flowers may have faced a more abundant and efficient pollinator community. Overall, the roles of pollinators and plants are not fixed in the communities, but are altered by the loss of other species (e.g. Dunne, Williams and Martinez, 2002; Kaiser-Bunbury *et al.*, 2010; Brosi and Briggs, 2013; Cirtwill *et al.*, 2018): the species adjust their interactions according to the available partners and their abundances, and the resources thus freed up may to some extent be used by other species. The fly species that I found to be particularly important at Zackenberg (*Spilogona sanctipauli*) is one of the few species which has not declined (Loboda *et al.*, 2017). Thus, its importance for pollination may have been accentuated with the decline of other flies.

Arctic communities have been spared from some of the environmental challenges of lower latitudes (e.g. intensification of land use, fragmentation of habitats or pesticides). Across most parts of the Arctic, the level of human activity is low and direct impacts (e.g. changes in land-use) are not necessarily threatening the ecosystems. On the other hand, the effects of climate warming are having an increasing impact in the area (e.g. Sturm *et al.*, 2001; Kattsov *et al.*, 2015; Schmidt *et al.*, 2016). While the communities sampled across latitudes in Chapter **II** did not show any strong latitudinal patterns, patterns of phylogenetic diversity suggest that the regional species pools are still recovering from the last glaciation. Indeed, I found phylogenetic diversity to be highest near past glaciation refugia. Given the constantly warming climate in the Arctic, it is likely that this past-glaciation dispersal of species continues at an increasing pace, and that species from lower latitudes are currently expanding towards the north (Sturm *et al.*, 2001; Bartomeus *et al.*, 2013). In my pan-arctic study (**III**), the diversity of flower-visitors increased with increasing precipitation and temperature. This further suggests that as the temperatures and precipitation increase along with a warming climate, new species will establish towards the north, and the overall species richness of arctic pollination networks will increase.

In general, the warming climate is making conditions less harsh for the species in the area, and potentially more suitable for a larger species pool. However, as we have seen at Zackenberg, such patterns may be complicated by interactions between tropic levels, with the phenologies of plants and pollinators potentially shifting out of synchrony (Schmidt *et al.*, 2016). The impact of such shifts in phenology could potentially be ameliorated through evolutionary adaptation of the species present, as well as by the dispersal of new species of more southern affinity towards the north. Nonetheless, given the rapid warming of the Arctic in general (Kattsov *et al.*, 2015) and especially of Zackenberg (Høye *et al.*, 2007), the species are probably struggling with the very rapidness of change. In addition, for Greenland as an island, the dispersal of new species is greatly limited by the surrounding areas of sea and ice.

While the pollinator communities have already declined both in the Arctic (Loboda *et al.*, 2017) and at lower latitudes (e.g. Biesmeijer *et al.*, 2006; Hallmann *et al.*, 2017), communities of flowering plants are yet to respond strongly to this. It is true that the arctic vegetation has already changed because of the effects of climate warming on environmental conditions (e.g. Sturm *et al.*, 2001; Myers-Smith *et al.*, 2011). However, changes in

flowering plant communities due to loss of pollinators are likely slow. For instance, many arctic plants are extremely long-lived. Even small scrubs such as *Dryas* can reach the age of a century (Kevan, 1972) and may retain a viable seed bank for at least decades (Cooper *et al.*, 2004). Thus, changes in the plant communities are lagging behind the quick responses of pollinators (Morris *et al.*, 2008). On the other hand, in an arctic-alpine site in Sweden, the diversity of pollinators has actually increased with an increase in habitat availability created by retreating glaciers (Franzén and Öckinger, 2012). However, this kind of effects were considered short-lived, as the arctic-alpine vegetation is replaced by species of warmer environments (Franzén and Öckinger, 2012).

In summary then, the response of flower-visiting communities to environmental change are generally fast given their rapid life-cycles. Plant communities are affected by both the environmental change and by changes in pollinator communities, but their responses are generally slower given their longer life-cycles and the existing seed-bank. As environments are changing world-wide causing rapid loss of biodiversity, a general decline of pollinators will likely impact pollination services (Cardinale *et al.*, 2012). In the context of crop production, these declines will likely cause losses, given that managed honey bees alone cannot mediate optimal yield (Goodwin, Cox and Taylor, 2011; Rucker and Thurman, 2012; Garibaldi *et al.*, 2013; Blitzer *et al.*, 2016). Competition for pollinators is likely to increase, with pronounced effects on wild plant species flowering at same time as mass-flowering crop plants are especially vulnerable.

4. CONCLUSIONS

In this thesis, I have identified *Dryas* as a key plant in the regional pollination networks, and as a key node tying together the whole Arctic ecosystem. I found arctic pollination networks to be surprisingly diverse, and I discovered that a large majority of the local insects were flower visitors. Despite large taxonomic diversity among flower visitors, I discovered that Arctic pollination networks were dominated by a few species only. At Zackenberg, most of the local insect species were attracted to *Dryas*, and thus *Dryas* accounted for practically all the insect-flower-visits and dominated the pollen loads on pollinators. However, only a single family and species significantly contributed to the seed set of *Dryas* at this most intensely-studied site. This supports the key inference that the sampling hypothesis is the main driver of a relationship between biodiversity and ecosystem functioning in pollination networks (Loreau *et al.*, 2001; Tilman *et al.*, 2001; Tilman, Isbell and Cowles, 2014).

In my work, I also detected strong competition for mutualistic partners among species on the same trophic level, i.e. plants competing for pollinators. The seasonal patterns observed in the strength of competition offer a new perspective on evaluating the effects of highly dominant flowering species in pollination networks. In the Arctic systems, the high abundance of *Dryas* determines the level of pollinator services available to other species and causes intra- and interspecific competition. Importantly, my results may partly reflect changes already occurring in the system. With an 80% decline in the abundance of the most important pollinators (muscid flies; Loboda *et al.*, 2017), and a concomitant phenological rift developing between pollinators and flowers (Schmidt *et al.*, 2016), the flowers of today may be facing a much less abundant and efficient pollinator community than the flowers of the 1990s. To what extent my results would have differed if I had conducted my study 30 years ago is an interesting but mostly unsolvable question. If the decline of pollinators continues (Loboda *et al.*, 2017) and the phenological mismatch increases (Schmidt *et al.*, 2016), it is likely that the competition patterns observed here become even more evident, which might result in poor pollination, seed set, and eventually in the decline of plant populations. Notably, similar patterns related to dominance and competition are likely found also in other ecosystems dominated by few species, e.g. in agricultural landscapes dominated by monocultures of crop plants and honey bees. As the climate warms, and as other environmental changes and the decline of pollinators continue, the survival of plant species may be challenged both in the Arctic and at lower latitudes.

Overall, my thesis work identifies an urgent need for research at two spatial scales: in the rapidly changing arctic environment, and in other pollination networks dominated by a few species.

At Zackenberg, causation of the recent decline of muscid flies to climate warming (or some other environmental change) versus to a phenological mismatch between plants and pollinators (Schmidt *et al.*, 2016) might be clarified by examining whether the decline has been stronger in particular fly species (e.g. the ones showing the largest mismatch with flowering). Added insights into the effects of *Dryas* on the other flowering species could

be gained by experiments manipulating *Dryas* densities and observing the structure of the pollination network and its functioning. As *Dryas* dominates the pollination network and causes pollinator limitation on plant community, the other flowering species are forced to adapt to avoid the flowering peak of *Dryas*. My thesis shows a phenological shift in the timing of *Dryas* and *Silene* along an elevational gradient, but it would be interesting to know how different densities of *Dryas* flowers impact the phenologies of other flowering species. Again, experimental manipulations of the densities of *Dryas* flowers, while recoding the performance of other flowering species, would give further insights into the effects of *Dryas* on the surrounding ecosystem.

In terms of agricultural landscapes, where pollination networks are dominated by a few species – just like they are in the networks that I have been studying in the Arctic – my findings should inspire the quest for imprints of two types: First, one should look for impacts akin to those detected for *Dryas*. Thus, one might determine what level of pollinators is needed for optimal pollination, so that intraspecific competition does not hamper crop yield. Second, one might address phenological effects of crop flowering. For instance, the global decline of pollinators may be stronger in species active during the flowering of crop plants (or the opposite, as they evade some of the pesticides). Meanwhile, in the wild plant community, species and individuals which are flowering during the peak of crop flowering are likely to be at a disadvantage compared to the ones flowering either earlier or later, thereby avoiding competition for pollination. Thus, a versatile exposure of the consequences of interspecific phenological differences may be essential to understand species extinctions of both plants and pollinators in multiple ecosystems.

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